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NOTES AND LITERATURE

HEREDITY

THE Fifth Report of the Evolution Committee of the Royal Society (London), like the preceding reports of this committee, is full of exceedingly interesting results of experimental work. Professor Bateson's committee is doing much to unravel the tangled thread of Mendelian inheritance. In the report in question I. B. J. Sollas gives the results of studies of color inheritance and of the inheritance of supernumerary mammæ in guinea pigs. The color factors recognized are:

G = factor for agouti ticking of the hairs.
B = factor for black pigment in eye and skin.
R = factor for red pigment in hair and red and chocolate pigment in eye and skin.
Ch = factor for chocolate pigment in hair, skin and eye.
C = factor for color.

Albinos with which he worked had colored points, hence in them the factor C was not absent, but either merely deficient or controlled in such a way as to confine color to the extremities.

The colored forms fall into two series—one black-eyed, the other ruby-eyed. In the series of black eyes we have the three color types agouti (GBRChC), black (BRChC) and red (BRC). In the ruby-eyed series we have cinnamon (GRChC), chocolate (RChC) and red (RC). The author is not entirely clear in the explanation of some of his formulæ. For instance, he offers no explanation why B does not occur in the hair of the red type in the black-eyed series. He does state, however, that in agoutis red spots occur because B fails to develop. Red spots occur also on black individuals for the same reason and on cinnamon individuals because of the failure of the chocolate pigment to develop. Each of the colors has one or more dilute forms.

The method of inheritance of supernumerary mammæ was not clearly made out. Several dwarf individuals occurred. Only one of these lived to maturity.

Miss Wheldale, in the same volume, gives further observations upon the inheritance of flower color in *Antirrhinum majus*. A chromogen (Y) allied to the flavone series of coloring matters appears to be the basis of color in these flowers. From this a yellow (xantheic) pigment arises which, when unmodified by ferments, gives rise to flowers with yellow lips, though the throat is ivory white. In some strains this yellow chromogen appears to be modified by a ferment (I) in such manner as to give flowers having both lips and throat ivory white (except for certain patches of yellow in the palate). An oxidase (L) acting on Y as modified by I gives a tinging of magenta color in the lips. L acting on Y in the absence of I gives crimson. A factor T, when present, causes the magenta color to extend from the lips into the tube. A factor D, probably also a ferment, deepens the shade of magenta, giving the color of the wild plant. D acts only in the presence of Y or I and L and T. Still another factor further intensifies the shade of color. Striping also occurs, the factor for striping being allelomorphic to D and recessive to it. There is also a concentration factor S. When S is homozygous the stripes are of an ivory background; when heterozygous the stripes are of a pale-colored background. Chemical studies indicate each of the color factors to be due to different definite compounds. An albino variety arises in the absence of Y. The albino is distinguishable from the ivory white.

Miss Marryatt, in the same volume, gives the results of the study of color inheritance in *Mirabilis Jalapa.* She finds a factor C for colored sap and a factor M which turns yellow sap red. One white strain was found to be lacking in both C and M. Another white strain had M but not C. The latter crossed with yellow gave red. The formula of the yellow strain was CCmm. The formula of the crimson strain was CCMM. Yellows heterozygote for C were paler in color than the corresponding homozygotes. Heterozygotes of the composition CcMM were magenta; those of the CCMm an orange-red, and CcMm magenta rose. The behavior of "flaking," a form of striping, was not fully made out.

Miss Wheldale also gives some very interesting results in another part of the report on the physiological interpretation of Mendelian factors for color in plants. White varieties of sweet peas and stocks were found to contain a colorless flavone (chromogen). Colored varieties are assumed to possess this chromogen in various stages of oxidation. Each shade of color appears, from chemical tests, to represent a distinct substance. Chemical studies of white and colored strains point to the following system of factors as the cause of color production: P is a peroxidase which sets oxygen free from X; X is a substance which functions as a peroxide; A is a ferment or oxidizer which reoxidizes X with atmospheric oxygen; C is a chromogen, the oxidation of which, by the combined action of A, X and P, gives anthocyanin. Additional factors, A_2, X_2 and P_2, similar in a general way to A, X and P, convert red into bluish-red and purple. Chemical tests indicate a shortage and not always entire absence of some of the above factors in white varieties. This bit of information is important in connection with the teleone theory recently proposed by the writer in an article in the AMERICAN NATURALIST, and accords with that theory.

Baur has recently published an extremely interesting report on his study of inheritance in *Antirrhinum*.[1] He gives some interesting details of methods with special reference to the avoidance of error in experimental work of this kind. He has found 22 unit characters, but deals with only 13 in this paper. Baur recognizes the following colors in *Antirrhinum:*

White = Miss Wheldale's white.

Yellow = Miss Wheldale's yellow.

Elfenbein = Miss Weldale's ivory. This differs from white by the presence of a pale-yellow chromogen, according to Miss Wheldale.

Rose-back; flesh-colored; chamois-rose; red; pale red; dark red; rubin.

The last six are superposed on yellow or ivory, and each of them may appear whole or as delilahs—that is, on lips only. The colors chamois-rose, red, dark red and rubin may also be striped (picturatum).

Baur recognizes the following color factors:

B (= Miss Wheldale's Y) is the basis of color.

bb is pure white, distinguished from ivory by absence of yellow in the throat.

B unmodified by other factors is yellow.

C in the absence of F (see below) converts B into elfenbein (ivory), and hence = Miss Wheldale's J.

F in the absence of R (see below) and in the presence of B causes a light rose color on the back of the flower, with a spot of similar shade on each side of the stem near the spur, giving Baur's rose-back type.

R with B and F gives flesh-color; but without B and F, R gives no effect.

M in the absence of A and the presence of B, F and R gives chamois-rose.

A in the presence of B, F, R and M gives red.

L in the presence of B, F, R, M and A, gives dark red. In the series of factors BFRMAL, each factor is dependent on all before it.

D spreads color from the lips over the tube. When D is absent all colored flowers have ivory or white tubes. D also makes the color of the lips more prominent. The factor D is independent of all previously mentioned factors.

G gives striping on colored ground.

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[1] E. Baur, "Vererbungs- und Bastardierungs-Versuche mit *antirrhinum*," *Zeitsch. f. Ind. Abst.- u. Vererb.*, 1910, Bd. III, H. 1 u. 2, pp. 34–98.

O gives red veins on ground containing no red. This factor shows in the presence of B, R, F and C, and may belong in the series BFRMAL between R and M. This point is not yet determined.

Q with B, F, R and M gives a peculiar shining rose color. It probably belongs in the above series after M, but may be identical with L.

Another factor gives a faded appearance to the edge of the lower lip of red flowers. There also appears to be a factor that governs the width of the yellow spot on the lower lip of red flowers. Investigation of four other factors which appear to affect flower color is in progress.

The author thinks there are possibly 20 factors concerned in flower color in *Antirrhinum majus.* Several factors not yet fully investigated influence the size of the flower, the relative size of the two lips, etc.

In addition to factors affecting flower color the following were made out:

E. When this factor is missing the flowers are radial (peloric).

P. The absence of P gives a peloric form different from that caused by E.

Another factor when absent gives a split corolla different from the normal zygomorphic form.

An apetalous flower is also known, but its inheritance is not worked out.

All of the flower color factors, except perhaps the one for striping, affect leaf color. There are also other factors which affect the intensity of red in the leaves. Two affect the green color. The absence of one of them produced the chlorina type previously mentioned in these notes. The absence of the other produced the aureas, also previously mentioned, and which are intensely yellow-leaved, being unable to grow.

The number of factors which affect leaf form are, for the most part at least, identical with those affecting the flower form, but are not yet fully investigated. The factors affecting the habit of growth are not yet fully worked out. Some of them seem to be identical with some of the flower-color factors. One character has been found that certainly does not Mendelize. This is a variegation conditioned by the cytoplasm. Only three of the factors studied are completely dominant; the others are incompletely so.

Baur, in another paper,[2] presents some very interesting evidence in favor of the hypothesis that the so-called graft hybrids are periclinal chimeras, the surface tissue being that of one parent form, the underlying tissue that of the other parent. Examples of such hybrids are *Cytisus Adami, Crataegus-*

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[2] *Ber. d. Deut. Bot. Gesellsch.,* Bd. XXVII, H. 10.

Mespilus graft hybrid, and H. Winkler's tomato-nightshade graft hybrid. The suggestion that the vegetative point of such forms consists of a more or less irregular mixture of the two tissues could hardly be true because one or the other tissue would soon gain the ascendency. Baur suggests that a careful study of mitosis in the vegetative point of such forms might settle the question.

East has recently published an interesting paper[3] dealing with the effect of selection on fluctuations. The conclusion is reached that neither the relative content of dry matter nor that of the nitrogenous matters of the potato can be changed by the selection of fluctuations and their subsequent asexual reproduction. In most potato fields there will occasionally be found plants which remain green after the main crop has matured and the vines died. East made a selection of plants maturing early and those maturing late, in some cases finding lateness or earliness reproduced in the selection, in others not. In one of these cases the long-lived plants selected from a variety were found to have pink sprouts, while a short-lived plant from the same variety had white sprouts. East suggests that either bud variation had taken place or that there had been an accidental mixing of two varieties.

There has been a good deal of work on selection for yield and other characteristics in old agricultural varieties, which indicate that bud variations or permanent mutations of one kind or another occasionally take place in such varieties, and that they gradually break up into a mixture of biotypes, which may differ in a considerable number of characteristics, including yielding power. Selection within such a variety might then result in the isolation of strains of better quality than the general average of the variety.

It seems to the writer that Dr. East has hardly given sufficient attention to the possibility of selection for improvement in old strains in which a considerable number of important mutations may have occurred. For instance, he says:

> As a result of these experiments I will not go so far as to say that variations in power of resisting physiological or fungus diseases do not occur in asexual reproduction, but I do believe that the relative probability that the commercial grower will obtain disease-resisting varieties by this means is negligible.

So far as newly isolated pure strains are concerned, the writer agrees very fully with this statement. There has, however, been a good deal of work which indicates that in old agricultural varieties variations have frequently occurred which render selection with a view to isolating the best strains present justifiable. Thus Waid, of the Ohio Experiment Station, Zavitz, of the Ontario Station, and L. G. Dodge, of the U. S. Department of Agriculture, have, by selection in old varieties of potatoes, obtained strains which outyielded the variety from which the selection was made. It is true the objection may here be urged that the supposed variety from which the selection was made was really a mixture, but this point is granted. The only question is as to how the mixture came about, whether by mutation or by mechanical mixture. It may not be possible to settle this question definitely because of the difficulty of proving the purity of an old variety; but the results that have been accomplished, it appears to the writer, do justify selection in old varieties with a view to isolating superior strains. After all, Dr. East would probably agree perfectly with the writer in what has just been said.

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[3] E. M. East, "The Transmission of Variations in the Potato in Asexual Reproduction," Connecticut Experiment Station Report, 1909–10, pp. 119–160, plates 1–5.

Concerning the character of bud variations, a number of which were found in East's work, the author gives it as his opinion "that practically all, if not quite all, bud variations are losses of a dominant, or epistatic, character allowing the appearance of a recessive, or hypostatic, character." He mentions four pink or red varieties that produced white variations that were constant the next season; also a purple variety produced a similar white variation. Several apparent changes from white to colored tubers appear, but they were not hereditary, and the varieties producing such variations had pink sprouts. Two varieties are mentioned in which changes of shape from long to round tubers occurred, the changes being permanent. Several other similar changes occurred but were not permanent. Change from shallow to deep eyes occurred in four varieties. In one case a peculiar change in the habit of growth of the tuber occurred, the peculiarity consisting in the formation of two tubers on the same rootstock at some distance from each other. This occurred in several varieties, but in only one case was it hereditary. It is not known whether the new type is recessive or dominant, but in the bud variations above discussed the new types are all recessive. The author suggests that these bud variations "seem to show that Mendelian segregation is not limited to the reduction division in the maturation sexual cell." It does not seem to the writer that this is a necessary conclusion.

Bud variations would certainly arise if Mendelian segregation occurred in somatic division, but they would also occur if for any reason a dominant character should become latent. It certainly yet remains to be demonstrated that they arise from Mendelian segregation in somatic tissues.

Kastle has recently published a very important paper in which he summarizes the results of investigations relating to oxidases and related compounds.[4] The paper is too extensive to permit of an adequate review at the present time. It has, however, a very important bearing on many Mendelian phenomena, and those who are interested in this subject will enjoy reading this excellent bulletin.

Guyer has recently given us a very thoughtful paper[5] on the possible relation of the chromosomes to hereditary characters. His argument is directed specifically against the Weismannian hypothesis of determinants. He does not attempt to minimize the importance of the nucleus in ontogeny or in heredity, but he is inclined to regard the development of what we call hereditary characters as a result of interrelations between the nucleus and the cytoplasm.

Speaking of experiments in which fragments of protozoa containing various proportions of the nucleus regenerated the organism, he says:

> If the nucleus is an aggregate of qualitatively different morphological units, one would expect parts to be missing in the regenerative protozoa in proportion to the amount of nuclear matter removed, but the evidence does not bear this out. The regeneration is seemingly complete, only a longer time is required if but a small fragment of the nucleus is left in the piece.

These experiments on protozoa disprove the determinant theory as held by Weismann, de Vries and others.

Guyer points out that the bulk of the fertilized egg is cytoplasm of maternal origin and that the developing organism must therefore be more of maternal than paternal origin.

> Nevertheless, we can see how the veneer of individual traits may be equally of maternal and paternal origin if, to express it crudely, we look upon cytoplasm and chromatin, respectively, as responsive mechanism and inciting agent, the character of the response depending both upon the constitution of the cytoplasm and the materials (enzymes? nutritive substances?) emanating from the nucleus.

[4] J. K. Kastle, "The Oxidases," Hygienic Laboratory Bul. No. 59, December, 1909.

[5] M. F. Guyer, "Deficiencies of the Chromosome Theory of Heredity," University of Cincinnati, Series 2, Vol. V, No. 3, September–October, 1909.

For many years the writer has held the view that in so far as the chromosomes have a relation to hereditary characters the influence they exert results from the relation they hold to the nutritive processes. He is therefore prepared to accept Guyer's views as expressed above.

Guyer gives a very striking analogy for the possible part which cytoplasm and chromatin may play in the development of specific characters.

> Any one of several species of insects may produce galls on a given plant, but each kind of insect always produces its own specific type of gall. Here is an actual case of living protoplasm producing a specific character through the activity of its specific exciting agent—that is, the reaction between certain secretions of the insect and the living substance of the plant produces new and definite structures.

Change either factor and the resulting structure must be modified.

> Likewise in the germ cell, alterations in the constitution of either chromosome or cytoplasm must undoubtedly produce structural changes in the adult.

He further points out that the chromosomes may be looked upon as the greater source of variability because they are derived in much greater proportion from the two parents than is the cytoplasm.

Guyer intimates that changes first initiated in the chromatin might be reflected on to the cytoplasm from time to time and there conserved. While it would seem to be possible that changes in the chemical constitution of a chromatin body might effect changes in other chromatin bodies and in the cytoplasm, I see no reason why such an assumption is necessary to account for permanent and fundamental evolutionary changes. I think we may look upon the cytoplasm and each of the chromosomes as having more or less of an individual existence and that each of them may undergo evolutionary changes in constitution more or less independently of the others, though, as above pointed out, a change in one of these cell organs might initiate changes in others. We may look upon the organism at any time as merely an expression of the complex relations then existing between the cytoplasm and the chromosomes and between the various chromosomes themselves. These relations are disturbed by any fundamental change in the composition or metabolic activities of any of these cell organs. For instance, the dropping out of a chromosome might not only change quantitative relations between various metabolic activities, but it seems possible that at least some of the chromosomes may possess characteristics which would give rise to qualitative changes, in case the chromosome should drop out. I have pointed out elsewhere[6] that in order to explain Mendelian phenomena on the basis of the behavior of chromosomes in the reduction division, it is not necessary to assume in the chromosome definite pangenes or determinants as separate entities. Each chromosome may take part in all phases of development. It is hardly probable that any particular chromosome, with the possible exception of a few of them, possesses exclusively characteristics necessary to the continued existence of the race in which they occur. In other words, speaking in a general way, each of the chromosomes may possess all the metabolic powers necessary to the race, while at the same time each chromosome may differ from others in minor particulars, giving rise to such differences as we see in Mendelian character pairs.

The writer does not quite follow Guyer in doubting the adequacy of the above interpretation of Mendelian phenomena, because in a few instances inheritance of a different type has apparently been found, but he does agree with him when he says:

> There are no sufficient reasons, I think, why we may not look upon their (the chromosomes') differences as differences of mere elemental, chemical and physical constitution rather than as differences among systems of determinate morphological units. . . . Even in case of the divorcement of particular parental chromosomes in gametes . . . it would seem that we might account for the so-called Mendelian phenomena by attributing to the chromosomes simply chemical and physical differences without endowing them with morphological entities.

Guyer points out that because the three elements carbon, oxygen and hydrogen condition substances of which they are components, we do not postulate a specifically determinative substance in any of them for each of the numerous carbohydrates and other products that result from their various combinations and arrangements. Similarly, we do not need to infer definite structural elements in the chromosomes, each of which is specifically determinative of a given character. It would seem more logical to assume that the differences between related organisms may be due to differences in the combinations of metabolic activities found in the various cell organs.

This paper of Guyer's accords very closely with the teleone theory of heredity propounded by the writer in the April number of the AMERICAN NATURALIST, 1910. It is gratifying to see that a number of biologists are coming to the view that the main facts of heredity can be explained without the assumption of any hypothetical units in the germ plasm. W. J. SPILLMAN.

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[6] AMERICAN NATURALIST, April, 1910.